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# INHERITANCE OF ENDOSPERM COLOR IN MAIZE[1]

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Few of the many characters in plants and animals studied by geneticists during the last seventeen years are now to be regarded as inherited in simple fashion. As more detailed and extensive studies on the heredity of each type of character, once regarded as a simple unit, are made, the more various the facts and the more complex the interpretations have become. The present paper describes such an increase in complexity of fact and interpretation in the heredity of endosperm color in maize, which at the outset was regarded as a single allelomorphic pair consisting of yellow and white, but which at present involves possibly as many as four pairs of factors, one of which brings about a dominance of white.

As studied and interpreted by Correns (3, 4) and Lock (10) and others, yellow endosperm in maize is determined by the presence of a factor for yellow, in the absence of which, the endosperm remains white. Lock (10) found various degrees of yellow among the grains classified as yellow, but all were easily separated from the white, so that he regarded them as fluctuations of slight importance, and, in his interpretation, did not distinguish between them. He notes, however, that on the average, homozygote yellows are deeper colored than heterozygotes. Lock studied very large numbers of $F_2$, $F_3$, and $F_4$ generation hybrid plants from crosses of yellow and white endosperm varieties. Back-crosses of the yellow heterozygote with the recessive white homozygote were also made in large numbers. The numerical results are very slightly vitiated by the technique used, but the numbers are so large as to make the small error from this source, in this particular case, of comparatively slight importance. Lock's results are summarized in Table 1.

Further studies by East and Hayes (5, 7), Burtt-Davy (1) and others on these endosperm colors brought to light a more complex state of affairs, for they found two yellow endosperm "colors" in maize, each behaving, when crossed with non-yellow (white) endo-

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[1] Brooklyn Botanic Garden Contributions No. 18.

TABLE I

| Cross | Yellow | White | Total | Ratios Act. Obt. | Ratios Theor. Exp. |
|---|---|---|---|---|---|
| Yellow heterozygote × white homozygote ($F_2$) | 1,963 | 1,982 | 3,945 | 49.6 :50.4 | 50:50 |
| Yellow heterozygote × pure white variety | 26,792 | 26,751 | 53,543 | 50.03:49.97 | 50:50 |
| White variety (homozygote) × yellow heterozygote | 2,723 | 2,846 | 5,569 | 48 :52 | 50:50 |
| Totals | 31,478 | 31,579 | 63,057 | 49.6 :50.4 | 50:50 |
| $F_2$ white segregate × pure white variety | 59 | all white | ears | | all |
| Yellow heterozygote (selfed) | 16,592 | 5,681 | 22,273 | 74.5 :25.5 | 75:25 |

sperm varieties, as an independent allelomorphic pair. In the varieties studied by East and Hayes, the two yellows were indistinguishable except that ears in which both were present in homozygous condition were usually darker than ears homozygous for either one of the yellows alone. Apparently either of the yellows, even in a homozygous condition, could not be distinguished from the other, but, when both were present in crosses with non-yellow races, the $F_2$ ratio approximated 15 Y : 1 W. Designating the two factors as $Y_1$ and $Y_2$, the presence of either produced a similar effect. In some crosses, dominance of yellow was complete and heterozygotes were indistinguishable, while, in other crosses, as many as five shades of yellow were present among the $F_2$ progeny, each shade signifying a difference in factorial composition from darker to light in the following order: $Y_1Y_1Y_2Y_2$, $Y_1Y_1y_2y_2$ or $y_1y_1Y_2Y_2$, $Y_1y_1Y_2y_2$, $Y_1y_1Y_2Y_2$ or $Y_1Y_1y_2Y_2$, $Y_1y_1y_2y_2$ or $y_1y_1y_2Y_2$. In Table 17, p. 56 (7) East and Hayes refer to an $F_2$ population from white × yellow endosperm which gives only a 3Y:1W ratio, but two shades of yellow are distinguishable—a dark and light in the ratio of 1 : 2. This is interpreted as a 1 : 2 : 1 monohybrid ratio in which the heterozygote is easily distinguished, owing to imperfect dominance. The nature of the starch, whether soft (flour) or horny (corneous), also causes a variation in the intensity of the yellow endosperm color. From certain crosses, in a few cases, apparently white segregate seeds, when planted, gave either pure yellow or 3 Y : 1 W progeny.

East and Hayes's data are partially summarized in Table 2:

TABLE 2

*Segregation of Endosperm Color in Maize*

| Cross | Yellow | White | Total | Ratios Act. Obt. | Ratios Theor. Exp. |
|---|---|---|---|---|---|
| $F_2$ generation of white×yellow or reciprocal or data on hybrid population of same character | 9,458 | 466 | 9,924 | 95.1: 4.9 | 93.8:6.2<br>(15:1) |
| $F_2$ generation of white×light yellow or reciprocal or data on hybrid population of same character | 6,792 | 2,428 | 9,220 | 73.7:26.3 | 75:25 |
| $F_2$ generation of white×dark yellow or reciprocal or data on hybrid population of same character | 2,376 | 766 | 3,142 | 75.7:24.3 | 75:25 |
| $F_2$ generation of white×yellow | 609 dark yellow:1,143 light yellow: 589 white | | | | |
| Expected | 585.2 dark yellow:1,170.4 light yellow: 585.2 white | | | | |

The varieties studied by Burtt-Davy (1) apparently consisted of two distinct yellow types—a dark and a light, each of which with its "opposite" represented an independent allelomorphic pair. The darker of these yellows gives a 1 : 2 : 1 ratio, while "the other (the paler) gives the ratio 9 : 3 : 3 : 1." The writer is at a loss to understand the meaning of the above quoted statement, unless the two yellows were crossed together and gave in addition to three types of yellow, whites in the ratio of 1 W : 15 Y. If each yellow is represented by an independent factor, crosses with white should give in each case in $F_2$ only 1 : 2 : 1 or 3 : 1 ratios. This pale yellow has sometimes been mistaken for a "dominant white." Burtt-Davy found ten shades of yellow in the $F_3$ seed generation from crossing yellows with whites. Further, Burtt-Davy (p. 172, 173, 177, 188) refers to a yellow endosperm color, which depends for its expression on the presence of two factors—a color factor and a pigment factor. In absence of either, the endosperm will be white, and by crossing two white races, each carrying one of the factors, the resulting progeny will all have yellow endosperm.

Emerson (8) obtained from $F_2$ populations of crosses of the orange yellow Queen's Golden with Black Mexican (white endosperm), two yellow endosperm colors (a dark and a pale) in addition to the expected orange and white endosperm segregates, and in $F_3$, some of the pale yellow segregates bred true, while others gave 3 pale yellow : 1 white.

Collins (2) reports a dominant white (albinistic) mutation in endosperm color. The mutation consisted of a single, wholly white ear which appeared in a field of a carefully selected strain of dark yellow dent with red cobs known as Gorham Yellow Dent.

The "albinistic" ear was fully matured, had white cobs, and the seeds when closely examined had a faint trace of yellow at the base, but would ordinarily be regarded as pure white. This white was evidently "dominant" over the Gorham Dent yellow, since the original mutant ear must have been in part, at least, cross-pollinated from the surrounding plants—all of which were Gorham Dent. The immediate descendants of this ear, either when selfed or cross-pollinated, consisted of both yellows and whites, the former greatly predominating. The yellows consisted of both dents and pale types, the former being the more numerous. Seeds of the three color types were grown. From 19 white seeds, 17 all white self-pollinated ears and two white tinged yellow ears were obtained. From 16 light yellow seeds were obtained 2 very light yellow ears, 11 ears with light yellow and white seeds approximating in many cases a 3 Y : 1 W ratio, 1 ear with dark yellow and white seeds approximating a 3 : 1 ratio, and 2 ears unclassified. Forty-nine dark yellow seeds produced 16 ears with yellow of varying shades, 22 ears with both yellow and white grains in the ratio of 3 : 1 (8,694 Y : 2,954 W), 4 ears with both yellow and white grains in the ratio of 15 Y : 1 W (2,548 Y : 177 W—theoretically expected 2,555 Y : 170 W), and seven ears with all shades from dark yellow to white. Crosses between a second generation progeny plant from the albinistic ear (presumably heterozygous for yellow and white) (no. 47) with two white seeded varieties of corn, in both cases gave ears with both white and yellow grains—the ratios approximating 1 : 1. Selfed yellows (44 seeds) from various ears of the first cross (no. 47 × White Dent) gave yellows and whites approximating a ratio of 3 Y : 1 W (44 ears with 16,351 Y : 5,184 W, theoretically expected 16,151 Y : 5,384 W). Selfed yellow seeds from the second cross (no. 47 × white Hopi) gave 2 ears with both yellow and white seeds, the yellow predominating and one "*pure white ear.*" Seeds of the selfed pure white ear gave 5 pure white ears and 4 faint yellowish tinted white seeded ears. No data are given as to cob color in the case of the second appearance of a white endosperm mutation, nor in the case of the dozen or more pure white ears obtained in later generations. Since both the white cob and white endosperm appeared together as a single mutation, it would be interesting to know whether they were inherited together, and whether the white cob color was also dominant over the red from which it sprung. Owing to ratio discrepancies, and the occurrence of traces of yellow in descendants of seeds classed as *pure* white, Collins regards the segregation of yellow and white endosperm color as incomplete or imperfect. In other words, factor contamination has occurred, though, in general, Mendelian ratios were obtained. Interpreting his results as showing the presence of at least two factors for yellow color and perhaps more, Collins regards as both "violent" and unwarranted. East (6, p. 404–405) however, in reviewing this paper, interprets Collin's data as demonstrating the presence of two factors for yellow endosperm color, one of which is much less effective in producing the yellow color than the other. East discredits the mutative reversal of dominance interpretation, suggesting the appearance of the original wholly white ear as due to non-development of color brought about by abnormal environmental causes, such as, perhaps, the "accidental presence" of some metallic salt in the soil. This suppression of color development, East intimates, is not extremely rare in experimental corn cultures.

## NEW DATA

The material consisted of an inbred strain of California Golden Pop with yellow endosperm and a strain of white endosperm maize obtained from Haage & Schmidt under the name of *Zea Caragua*.[2] The latter bred true to a white endosperm intermediate between flour and corneous in texture. A white endosperm variety of Hopi maize, isolated from seed obtained from G. N. Collins, was also used.

In classifying the colors of the $F_2$ and $F_3$ seeds, three methods were used—(1) each seed as classified on the ear, was picked off and transferred to a black velvet background and contrasted either with the parental varieties or with other pure white and yellow races; (2) most of the seeds were classified independently by the writer and his assistant Miss M. Mann; (3) both the writer and Miss Mann reclassified many of the $F_2$ and $F_3$ ears twice, first by re-examining both the yellow and white groupings of each ear and second by mixing the two color groups together again and reselecting. In each reclassification, the ratios resulting from previous classifications were unknown. These determinations were fairly accurate as demonstrated by the $F_2$ classification and its $F_3$ progeny. In some cases a photographic blue ray screen was used.

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[2] Described by Sturtevant (11). Apparently an old variety desseminated in Europe by Vilmorin.

### $F_1$ GENERATION PROGENY

California Golden Pop pollinated by *Zea Caragua* gave uniformly white endosperm grains with perhaps the very faintest suggestion of yellow.[3] This cross was repeated six times with similar results. The reciprocal cross has not yet been obtained. Crosses of Golden Pop pollinated with white endosperm Hopi gave similar results.

### $F_2$ GENERATION

Three independent classifications of the $F_2$ progeny from California Golden Pop × *Zea Caragua* are given in Table 3. The first three ears were classified with the aid of a photographic blue ray screen.

TABLE 3

*Endosperm Color of $F_2$ Progeny of (Z 14×Z 21)*

| Progeny No. | 1st Classif. | | 2d Classif. | | 3d Classif. | | Total Grains |
|---|---|---|---|---|---|---|---|
| | White | Yellow | White | Yellow | White | Yellow | |
| (Z 14×Z 21)—1 | 254 | 82 | Practically the same | | — | — | 336 |
| ( “ “ )—2 | 264 | 108 | | | — | — | 372 |
| ( “ “ )—3 | 285 | 89 | “ | “ | — | — | 374 |
| ( “ “ )—4[4] | 257 | 79 | 235 | 101 | 225 | 111 | 336 |
| ( “ “ )—5[4] | 346 | 73 | 319 | 100 | 267 | 152 | 419 |
| ( “ “ )—6[4] | 338 | 98 | 358 | 79 | 340 | 96 | 436 |
| ( “ “ )—7[4] | 346 | 77 | 316 | 109 | 259 | 166 | 425 |
| ( “ “ )—8[4] | 248 | 70 | 235 | 82 | 214 | 104 | 318 |
| ( “ “ )—25*a* | 350 | 146 | 311 | 185 | 354 | 142 | 496 |
| ( “ “ )—25*b* | 358 | 129 | 350 | 137 | 339 | 148 | 487 |
| ( “ “ )—26*a* | 422 | 126 | 420 | 128 | 410 | 138 | 548 |
| ( “ “ )—26*b*[5] | 494 | 109 | 483 | 121 | 472 | 132 | 604 |
| ( “ “ )—28 | 336 | 91 | 318 | 109 | 315 | 112 | 427 |
| ( “ “ )—29*b* | 478 | 131 | 460 | 149 | 438 | 171 | 609 |
| ( “ “ )—30 | 390 | 143 | 406 | 127 | 388 | 145 | 533 |
| ( “ “ )—31 | 373 | 54 | 313 | 114 | 316 | 111 | 427 |
| ( “ “ )—32 | 332 | 104 | 332 | 104 | 331 | 105 | 436 |
| ( “ “ )—33 | 427 | 73 | 371 | 129 | 386 | 114 | 500 |
| ( “ “ )—34*a* | 221 | 52 | 209 | 64 | 211 | 62 | 273 |
| ( “ “ )—35 | 309 | 93 | 295 | 107 | 280 | 122 | 402 |
| ( “ “ )—36 | 375 | 95 | 379 | 91 | 369 | 101 | 470 |
| ( “ “ )—37 | 338 | 97 | 328 | 107 | 282 | 153 | 435 |

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[3] The $F_1$ white endosperm ot these seeds is indistinguishable from that of seeds of several of the well known smooth white seeded varieties of pop-corn, when compared with them. From data on non-guarded crosses referred to later, the reciprocal cross probably gives the same results, except the endosperm is opaque white instead of translucent white.

[4] Ears obtained from unbagged $F_1$ plants allowed to intercross with other $F_1$s of similar pedigree.

[5] One unclassified.

Owing to the increased experience, the third classification given in Table 3 is probably the most accurate. Assuming that it is, from a total of 9,663 progeny, 6,999 were classed as white and 2,664 as yellow. On the assumption of a one-factor difference between the two maize races with complete or practically complete dominance of the white color, the theoretically expected numbers would be 7,248 W : 2,416 Y (3 : 1). The deviation between the ratio actually obtained and that theoretically expected is 249. The yellow segregates were far from uniform in color, all shades from a dark yellow (not orange) to a very light lemon yellow were present on the same ear. Further, in some ears, the yellow was principally confined to the base of the grain, nearest the point of attachment. A few dark yellow grains were somewhat deeper colored than the yellow grand-parental California Pop, but this may be due to segregation of various factors that effect endosperm texture, as the dark yellow grains usually appear less translucent than those of the grand-parental Pop variety.

## BACK CROSSES OF $F_1$ WITH Z 21 (THE DOMINANT WHITE ENDOSPERM PARENT)

(Z 14 × Z 21)–29a × Z 21......All white
(Z 14 × Z 21)–34b × Z 21......All white

These two ears, resulting from back crosses of the $F_1$ with the dominant endosperm parent, came from two $F_1$ plants which also produced two selfed ears (29*b* and 34*a* in Table 3). The back-crossed ears were uniform in seed color, the white being more opaque than in the endosperm of the $F_1$ grains. Nos. 29*b* and 34*a* gave typical $F_2$ ratios and the yellows were of several shades as in all the other ears with $F_2$ seeds.

## $F_3$ GENERATION

From self-pollinated ears Nos. 1, 2 and 3 (Table 3) of the $F_2$ generation, approximately 1,000 plants with $F_3$ endosperm seeds were grown. Of these, 43 ears were self-pollinated, 27 of which came from $F_2$ seeds classed as white, and 16 from $F_2$ seeds classed as yellow. Nine of the white seeds gave all white $F_3$ progeny, while 19 gave both white and yellow grains approximating the ratio of 3 W : 1 Y (Table 4). The 16 $F_2$ seeds classed as yellows gave 14 all yellow ears, and 3 ears with both white and yellow seeds approximating the ratio of 3 W : 1 Y.

TABLE 4

$F_3$ *Progeny of White-Seeded* $F_2$ *Heterozygotes* (*Z* 14×*Z* 21)

| Plant No. | White | Yellow | Total No Grains |
|---|---|---|---|
| 1 W—63 | 269 | 55 | 324 |
| 1 W—89 | 294 | 98 | 392 |
| 1 W—90 | 119 | 38 | 157 |
| 1 W—91*a* | 277 | 122 | 399 |
| 1 W—93 | 364 | 88 | 452 |
| 1 W—98 | 233 | 74 | 307 |
| 1 W—99 | 298 | 108 | 406 |
| 1 W—101 | 298 | 140 | 438 |
| 2 W—66 | 309 | 75 | 384 |
| 3 W—43*a* | 113 | 48 | 161 |
| 3 W—43*b* | 190 | 90 | 280 |
| 3 W—48 | 143 | 70 | 213 |
| 3 W—49 | 119 | 39 | 158 |
| 3 W—52 | 343 | 104 | 447 |
| 3 W—53 | 216 | 56 | 272 |
| 3 W—56 | 59 | 22 | 81 |
| 3 W—57 | 417 | 72 | 489 |
| 2 Y—77*a*[6] | 212 | 78 | 290 |
| 2 Y—77*b*[6] | 245 | 81 | 326 |
| 2 Y—84[6] | 185 | 47 | 232 |
| Total actually obtained | 4,703 | 1,505 | 6,208 |
| Total theoretically expected | 4,656 | 1,552 | 6,208 |

Both yellow and white endosperm colors varied markedly in this generation. In the case of white endosperm, the differences were largely due to segregation of factors affecting the texture and degree of translucency and opaqueness. Many ears had opaque caps, while the remainder of the endosperm was corneous. In such cases, the yellow was most apparent in the corneous region. Translucent whites such as one finds among popcorn varieties always appear slightly yellow when contrasted with opaque whites such as are found among the dent and wax varieties. No selfed ears were obtained of a deeper yellow color than that in the California Pop ancestor. The all yellow ears were of at least three distinguishable types: (1) a very light translucent lemon yellow, (2) a yellow as dark as the ancestral yellow and (3) a yellow with opaque whitish caps.

## UNBAGGED EARS OF Z 14 AND Z 21

Unbagged ears on plants of Z 14 grown close to varieties with deep yellow or orange endosperm color invariably have a large number of dark yellow or orange grains, from which the dominance of these yellows over that of Z 14 (California Pop) is to be inferred, as bagged ears are always of a uniform medium yellow.

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[6] $F_2$ seeds probably wrongly classed as having yellow endosperm.

Unbagged ears of Z 21 (*Zea Caragua*) on plants grown under conditions similar to those mentioned for Z 14 have never been found in my cultures with yellow grains. Further, cultures of Z 21 grown alongside of $F_1$ and $F_2$ generation hybrids (Z 14 × Z 21) have always produced (in my experience) only white ears. The Z 21 cultures bloomed at about the same time as many of the hybrids, so that the difference in flowering time would not account for the absence of yellow grains.

## INTERPRETATION

In the light of the preceding data, endosperm color differences between Z 14 (California Pop) and Z 21 (*Z. Caragua*) may be regarded as due to the presence and absence of a single factor A. The presence of A prevents the development of the yellow color, when the factors for yellow pigment are present, and gives no indication of its presence in a variety from which these factors are absent. In the absence of A, a given variety may be either yellow or white. In respect to this factor A, then, and a single factor for yellow pigment, varieties of corn may be of four kinds:

(1) AAYY (white endosperm)
(2) AAyy (white “ )
(3) aaYY (yellow “ )
(4) aayy (white “ )

Crossed with each other, these should give:

| Cross | $F_1$ | $F_2$ |
|---|---|---|
| 1(W)×2(W) | white (AAYy) | all white |
| 1(W)×3(Y) | white (AaYY) | 3 W:1 Y |
| 1(W)×4(W) | white (AaYy) | 13 W:3 Y |
| 2(W)×3(Y) | white (AaYy) | 13 W:3 Y |
| 2(W)×4(W) | white (Aayy) | all white |
| 3(Y)×4(W) | yellow (aaYy) | 3 Y:1 W |

So far as the data on Z 14 × Z 21 are concerned, California Golden Pop would be represented on the above scheme as aaYY, while the formula AAYY would be the only one applicable to Z 21 (*Z. Caragua*). All of the common white endosperm varieties of corn which are wholly or partially recessive to yellow endosperm color have the formula aayy, neither the suppression nor the pigment factor being present.

First generation ($F_1$) progeny from crosses between whites such as 1 × 4, or whites and yellows such as 2 × 3, should give, when backcrossed with white endosperm aayy (4) plants, white and yellow endosperm seeds in the ratio of 3 W : 1 Y. In other words, two whites crossed together in $F_1$ give a certain proportion of yellows. The obtaining of such results in partially worked out experiments on heredity of endosperm color, in which it was taken for granted that white endosperm color was always recessive, might be temporarily interpreted as due to the presence of a color factor in a heterozygous condition in one of the races experimented with. Perhaps Burtt-Davy's statements regarding the presence of a color factor for endosperm (1, pp. 172, 173, 177) resulted from an experiment of this type. I have not had access to papers with the data on which these statements are based.

The preceding discussion assumes only one factor for yellow endosperm pigment, whereas East and Hayes, Collins and Burtt-Davy have each found at least two such factors. Further, Emerson and East (9, p. 11) suggest that orange endosperm color, such as is characteristic of Queen's Golden Pop, Tom Thumb Pop, Yardstick and some Chinese varieties (much intensified), is due possibly to the presence of a color intensifying factor. The $F_2$ and $F_3$ data on crosses of Z 14 × Z 21 show the presence of other color modifying factors, especially one which dilutes ordinary yellow to a very pale lemon color. Other investigators have also obtained this type.

## SUMMARY

1. Crosses of a yellow endosperm variety of maize (California Golden Pop) with a white endosperm variety (*Z. Caragua*) gave uniformly white progeny in $F_1$ and a ratio approximating 3 W : 1 Y in $F_2$. The $F_2$ generation white grains, when planted, gave either all white $F_3$ generation progeny or a mixture of white and yellow grains approximating a ratio of 3 W : 1 Y. The $F_2$ yellow grains, except in two cases, produced all yellow $F_3$ self-pollinated ears. The yellow grains in both the $F_2$ and $F_3$ generations varied considerably, and, in $F_3$, ears wholly of *very* light lemon yellow grains were obtained. Unprotected ears of Z 21 in close proximity to varieties and hybrids having yellow endosperm always gave wholly white endosperm ears.

2. These results are interpreted as mainly due to the presence and absence of an endosperm color suppression factor A. A factor Y for yellow pigment is present in both races studied. *Zea Caragua* (Z 21) is to be regarded as homozygous for both A and Y, while California Golden Pop (Z 14) is homozygous for the presence of Y and the absence of A.

3. The segregation of other endosperm factors, such as those for flint and floury texture, opaque caps, etc., also modified the endosperm color expressions.

4. Including the suppression factor A, at least three and possibly five pairs of factors are primarily responsible for endosperm color in maize.

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